Abstract  This study examines the relationship between cladoceran species richness and ecosystem functioning. I conducted an experiment in which four cladocerans, *Daphnia magna*, *D. longispina*, *D. pulex* and *Chydorus sphaericus*, were cultured in microcosms using different species combinations and levels of species richness. The results demonstrate that even within this closely related group of organisms the effects on ecosystem-level variables, such as total algae and zooplankton biomass, per capita productivity, and nutrient concentrations, as well as phytoplankton community structure, were highly variable between different combinations of these species. Since only four species were involved in this study, species-specific effects dominated the general relationship between species richness and ecosystem functioning. Particular combinations of species resulted in effects that indicated more efficient grazing. These effects, which were most pronounced in combinations including both *D. magna* and *C. sphaericus*, were manifested as an indirect effect as the prey community shifted towards grazing-resistant species. As a result, the productivity of the prey community decreased, because phytoplankton species with lower per capita productivity became more dominant. I suggest that the primary mechanism that caused this significant effect was complementarity in prey-size use of *D. magna* and *C. sphaericus*. In terms of prey-size range, *D. pulex* and *D. longispina* were redundant when *D. magna* was present and were quickly outcompeted by the latter despite higher per capita filtering efficiency. The results show that different mechanisms are important for different combinations of species. Furthermore, the ability of the prey community to respond to changes of consumer species composition is an important factor in experiments in which consumer species richness is experimentally manipulated.

Key words  Biodiversity · Ecosystem functioning · Redundancy · Complementarity · Trophic interactions

Introduction

Ecosystem-level effects of experimental manipulations of species richness have been reported frequently during the last 5 years (e.g., Naeem et al. 1994; Tilman et al. 1996; McGrawy-Steed et al. 1997; Wardle et al. 1997; van der Heijden et al. 1998; Hooper 1998; Mikola and Setälä 1998; Naeem and Li 1998). Studies that test experimentally for the effect of species richness have manipulated the number of species at several trophic levels simultaneously (Naeem et al. 1994; McGrawy-Steed et al. 1997; Naeem and Li 1997, 1998), the number of primary producers (Hooper and Vitousek 1997; Tilman et al. 1996,1997a), or the number of prey items (Lundstedt and Brett 1991; Bernays and Minkenberg 1997; Balču nas and Lawler 1995). A few studies have specifically investigated the effects of predator-prey interactions by manipulating only the number of predator species (Morin 1995; Mikola and Setälä 1998; Naeem 1998). In comparison to diversity experiments with plants, in which the resource is abiotic, this is a particularly interesting aspect because of the potential for the living prey community to respond to changes at the consumer level.

The hypothesized relationships between biodiversity and ecosystem level properties, i.e., the redundant species hypothesis, the rivet hypothesis, the idiosyncratic hypothesis, and the null hypothesis (reviewed in Lawton 1994; Naeem et al. 1994; Naem 1998; Schläpfer et al. 1999) serve mainly as heuristic devices to facilitate and sharpen the debate (Lawton 1994). However, from the growing body of experiments, some conclusions can be drawn regarding the mechanisms behind the relation between diversity and ecosystem function. First, functional differences between species are the key to understanding...
the ecosystem function of biodiversity (Naeem et al. 1995; Tilman et al. 1997b; Grime 1997; Lawton et al. 1998; Hodgson et al. 1998). Second, three types of mechanisms have been repeatedly emphasized as important: the “sampling” or “species composition” effect (Tilman et al. 1997a; Loreau 1998; Tilman 1998), overlap of resource niches or redundancy (Walker 1995; Mikola and Setälä 1998; Naeem 1998), and complementarity in resource niches or total resource range utilized by a guild of species (Tilman et al. 1997b; Hooper 1998; Mikola and Setälä 1998). Furthermore, the possibility of complex interactions between species which may cause unexpected responses when species are removed from or added to a community has been advocated (Lawton 1994; Jones et al. 1997; Kareiva and Bertness 1997; Tilman et al. 1997b). Different combinations of these mechanisms may give rise to different effects, and when averaged over many replicates with independent combinations of species, may reveal what mechanism dominates the relationship between species richness and ecosystem-level process in a particular type of ecosystem.

Mikola and Setälä (1998) adapted the rivet hypothesis for systems containing several trophic levels. Their main objection was that the rivet hypothesis predicted a monotonic decline in ecosystem functioning with decreasing species richness, whereas many other relationships may be expected in multi-trophic systems. Thus they called the reformulated hypothesis the “predictable change hypothesis” because it requires a priori knowledge of the control of trophic level biomasses in a system. In pelagic habitats, much is known about the control of trophic level biomasses from trophic manipulation experiments in which zooplankton biomass was controlled by trophic manipulations (Sterner 1989; Brett and Goldman 1997; Pace et al. 1998). From these studies we have learned that increasing zooplankton grazing pressure decreases autotrophic biomass and increases dissolved nutrient concentrations. In addition, a shift in the phytoplankton community towards grazing-resistant species is commonly observed (Kerfoot et al. 1988; Strong 1992; Metaxas and Scheibling 1996). Cladoceran zooplankton are important components in freshwater ecosystems and much is known about different species autecology (Carpenter et al. 1985). The present paper reports the first experiment in which cladoceran zooplankton species richness is directly manipulated. I specifically investigate the resource-consumer interaction by manipulating species richness and combination at the consumer level. In order to investigate the mechanisms for observed changes, I have chosen species that coexist in nature and for which niche width (measured as the range of prey size) and resource harvest efficiency (grazing rate) are well known. In addition, I specifically investigate the response of each phytoplankton species as well as the collective properties, phytoplankton biomass and productivity. Assuming that increasing cladoceran species richness increases the efficiency in resource use of this organism group (i.e., grazing rate and/or prey-size range) the effects mentioned above should also manifest themselves as species richness increases. Thus, these are the predicted changes with increasing cladoceran species richness in this study.

The aims of this study were (1) to test which of the proposed hypotheses conforms to the general relationship between cladoceran species richness and ecosystem-level measures, (2) to investigate which species combinations contribute to this relationship, and (3) to understand the causal mechanisms.

Material and methods

Choice of species

The particular cladoceran species used in this study were selected because they are, to a large degree, non-selective feeders (DeMott 1986), somewhat like different sized vacuum cleaners, and have a large overlap in resource demand. This is particularly true for three daphnids, *Daphnia magna* (Strauss), *D. longispina* (Muller), *D. pulex* (De Geer), and a chydorid, *Chydorus sphaericus* (Muller) (see Lundstedt and Brett 1991). All species used are known to coexist at least temporarily in rockpools along the Swedish east coast (Bengtsson 1989; Ranta et al. 1993). Some important characteristics of these species that determine the range of resources that they can exploit and the efficiency thereof are shown in Fig. 1 together with the approximate sizes of prey found in this study. I will refer to the overlap of resource-sizes utilized (or the fraction of prey-sizes shared) as redundant function in the following text. Complementarity, on the other hand, is a measure of the total range of prey-sizes utilized by a guild of species (e.g., Hooper 1998).

Experimental design

The four species used in this experiment, *D. magna* (M), *D. longispina* (L), *D. pulex* (P) and *C. sphaericus* (C), provide 16 possible species combinations. To test for differences between species com-